Euphorbiaceae – a new host-plant family for *Carcharodus alceae* Esper, 1780 (Lepidoptera: Hesperiidae) and a discussion on the use of Euphorbiaceae by butterfly larvae (Papilionoidea, Hesperioidea) in the world

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Abstract. *Carcharodus alceae* is one of the most common and best known of the European hesperiids; its Malvaceae host-plant family was already known to Esper in the 18th century. *Chrozophora tinctoria* (L.) Raf. (Euphorbiaceae) was found to be both a new food-plant species and family for this hesperiid. Late-season use of this new host-plant by *C. alceae* may have its disadvantages as the plant does not afford adequate protection for the overwintering pupa. This is the first record of a host-plant for *C. alceae* that does not belong to the mallows; it is also the first record of a Palaearctic hesperiid feeding on Euphorbiaceae. The discovery, the biology of the skipper and the use of euphorbs by other butterflies in the world are presented and analysed.

Key words. *Chrozophora tinctoria*, Euphorbiaceae, host-plant, *Carcharodus alceae*, Hesperiidae, Palaearctic, Israel, Middle East.

Introduction

The species *Carcharodus alceae* was described as "*Papilio alceae*" by Esper in 1780 from Erlangen, South Germany. He named it after its host-plant the "*alcea rosea ... Gartenmalve*" (= *Althaea rosea*), otherwise known as the Common Hollyhock. It became the type species of the genus *Carcharodus* Hübner, 1819 by ICZN's opinion number 270 of 1954.

The butterfly is widely distributed in Southern and Central Europe up to 52°N and stretches eastwards across Turkey, the Middle East, the Caucasus, northern Iran, Turkmenistan, Uzbekistan, Kazakhstan, Afghanistan, and the Altai Mts. to East Siberia. Isolated populations of this Palaearctic skipper exist in the Sinai Peninsula (this is a recent isolation, Dr Rienk de Jong checked the genitalia to find that it is a 'normal *Carcharodus alceae*') and Yemen, as a distinct subspecies *wissmanni* Warnecke, 1934. The closely related *Carcharodus tripolinus* (Verity, 1925) (de Jong 1978), flies in the southern part of the Iberian Peninsula as far north as Murcia province, Spain and about 140 km north of Lisbon in Portugal (de Jong pers. comm.). In North Africa it extends from Morocco eastwards to Tunisia and Libya. Throughout their range, both species have always been associated with Malvaceae host-plants as evidenced by citations in numerous publications. The story is now known to be incomplete with the present record of an additional and exceptional host-plant family, the Euphorbiaceae.

The discovery

In mid-March 1988 a diapausing winter larva of *Carcharodus alceae* was found in Bet Arye, resting in typical fashion inside a folded leaf of *Alcea setosa* (Boiss.) Alef. (Malvaceae). An adult female emerged on 15 April 1988. Subsequently, on 14 May

1988, three eggs were found on small, stellate (star-like), hairy leaves of *Malvella sherardiana* (L.) Jaub. et Sp. (Malvaceae). This prostrate, new host-plant for Israel, appeared in my garden on alluvial soil which was imported from coastal lowlands. The larvae found difficulty in surviving on the small leaves, which did not provide sufficient shelter and, indeed, they all succumbed to parasitic braconid wasps. On 23 July 1988, I found eggs again on *M. sherardiana*. On 6 August 1988, I found small *C. alceae* larvae inside folded leaves of a third host-plant that grew next to the *Malvella* on the same black soil. The greyish leaves were large enough to provide shelter for the growing larvae but, when taken indoors for closer observation, the larvae were seen to reject this foodplant and quite often I found them wandering off the plants looking for other food. None of the larvae survived. Attempts were made to identify this unknown host-plant, which was covered with stellate tiny hairs but had no fruits at the time, it was provisionally considered to be *Glinus lotoides* L. Molluginaceae. (A resting *C. alceae* female was photographed in Cyprus on *Glinus lotoides* (Makris 2003: 272); following my request, Christodoulos Makris tried in late summer 2004 to find larvae of *C. alceae* within leaf pods of *Chrozophora* and *Glinus* plants, but it was too late in the season to find evidence of feeding). On 22 September 1990, a search was made in the public gardens of Bet Arye, where an irrigated area, originally prepared for the planting of flowers but later abandoned, allowed the invasion of various wild plants including various Crucifers, *Echinochloa colonum* (L.) Link, *Malva* sp. and *Chrozophora* sp. A thorough search for larvae ended successfully with one L4 *C. alceae* larva, 15 mm long, found inside a leaf pod on *Chrozophora tinctoria* (L.) Raf. (Euphorbiaceae). On 10 October 1990, the first observed *C. alceae* adult to complete its life cycle on *C. tinctoria* emerged successfully. It is important to note that the neighbouring *Malva* was devoid of larvae and that *Chrozophora* was apparently preferred as a host-plant.
No other butterfly is known to feed on this newly discovered Euphorbiaceae host-plant and thus *C. alceae* becomes the first butterfly (Rhopalocera) reported to feed on *Chrozophora tinctoria* (Robinson et al. 2004; Fiedler 1991 & pers. comm.).

The life history of *Carcharodus alceae*

The species is on the wing in Israel from February in the Negev until November in the Mediterranean region. In the South Sinai Massif it flies from March until September, and in Mt Hermon from the end of May at 1500 m to July-August at 2000 m. It has up to three annual broods depending upon the elevation above sea level and availability of host-plants.
Eggs and laying preferences. Eggs are laid singly on both surfaces of the leaves of *Alcea setosa*, its most common host-plant in Israel. The egg is brown when laid and is 0.75 mm in diameter and 0.6 mm high. Its spherical surface is covered with relatively few but tall bulges that may provide partial protection from parasites. These nodes converge upwards to create five prominent ridges, the tops of which circle the depression of the micropyle. Its typical texture, with a "flower" of 8–9 "leaves" around the micropyle is shown on Fig. 2. In mid-September 2004 three types of hollyhock were growing in my garden: 1) Wild, 2) Hybrids of wild x cultivated, and 3) Cultivated. Eggs

Fig. 1. *Chrozophora tinctoria*, the new host-plant of *Carcharodus alceae* at Kibutz Haogen, Hasharon district, Central Coastal Plain, Israel, 19.ix.2003 (circled: a leaf pod of *C. alceae* larva).

were laid only on the wild plants, at the base of the dry flower stalks where few green leaves still existed. The females totally ignored the other *A. setosa* plants which carried fresh and larger leaves. Only when the few leaves of the wild plants were consumed did the females start to lay on the hybrids. The cultivated *A. setosa* were not visited by any female and remained unused. It is quite astonishing that the *C. alceae* females could sense exactly, and with no mistake, which plant they preferred. Does it mean that these three types of plants are chemically different?

L a r v a e . The young larva hatches usually after five to seven days; it opens a hole in the upper side of the egg by cutting around and lifting the "flower" mark. It does not consume the egg shell and immediately cuts and/or folds a leaf to prepare its sheltered leaf pod (Figs. 1, 3, 4). It is 2 mm long, light green with short hairs, with a black head and a reddish "collar" behind the head. It grows to about 23 mm long and at this stage of development its body is whitish-green with bright short hairs. The head remains black and is covered with tiny brown and yellow setae, the "collar" is black with three yellow spots (Fig. 5). In mid-summer a larva which hatched on 22 July pupated 24 days later, on 15 August.

In July 1979 I bred, simultaneously, larvae from the isolated population around Santa Katarina Monastery, 1600 m, in the Southern Sinai Massif and from Yahud (10 km east of Tel Aviv, Israel, elev. approx. 100 m). I noticed slight differences in larval coloration; the Sinai larvae were usually much brighter.
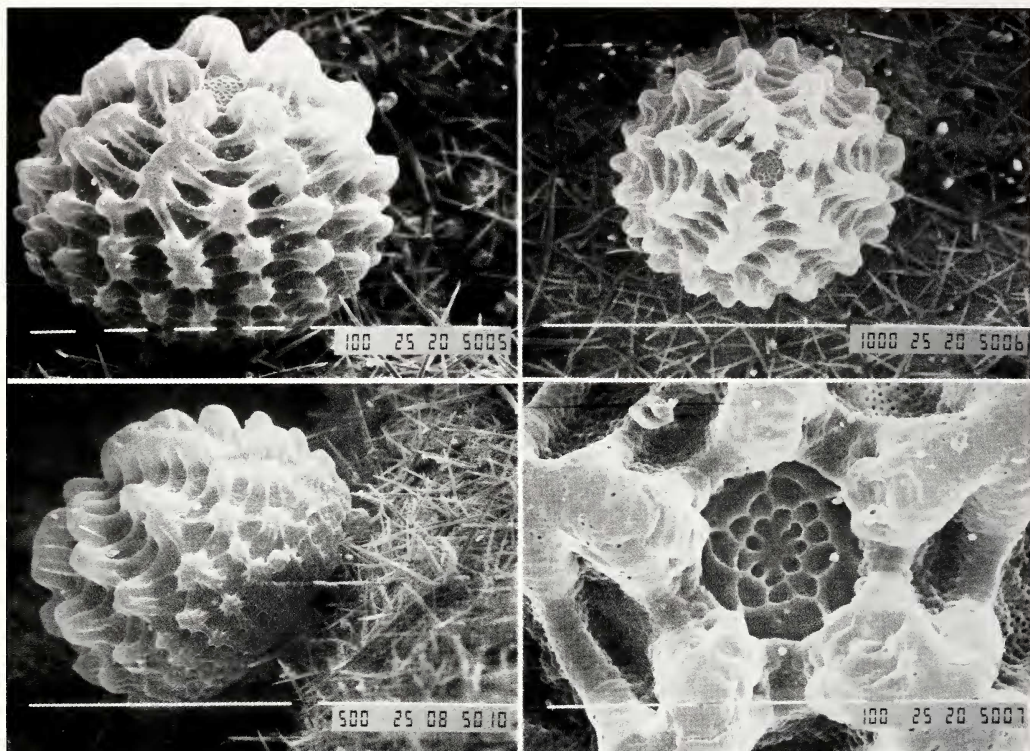
Fig. 2. *Carcharodus alceae* egg SEM (Scanning Electron Microscope) photographs (photo: Dr. Leonid Shikmanter).

P u p a . Pupation takes place inside the leaf pod (Fig. 6), the pupa being attached by means of the cremaster, sometimes with an additional thoracic girdle. It is up to 16 mm long, 5 mm in diameter, brown, and covered with white powder. The eyes and the spiracles are black. In August it hatches after 8–10 days (Fig. 7). On 21 February 1992, at the end of an exceptionally cold and wet winter, an overwintering L4 larva, 18 mm long, was found inside a leaf pod of *Alcea setosa* in Bet Arye, 310 m. It pupated on 15 March 1992, with the adult hatching a month later on 14 April 1992. On one occasion a winter-diapausing larva, which was found in Dvira, Northern Negev on 7 February 1981 inside an *A. setosa* leaf pod, emerged in July having spent some four months aestivating in the pupal stage.

D i a p a u s e . I noted three variations of diapause:

1) The autumn larvae of the final summer brood enter winter diapause which lasts until February in southern warmer localities, and until April in the central Mediterranean plateau. This is the only form of diapause reported until now in numerous books and other publications.

2) A pupal summer aestivation, spanning March to July, was found only once in a Northern Negev population (details were given above).

3) Winter pupal diapause – Two fully-grown larvae were found on 19 September 2003 inside leaf pods on *Chrozophora tinctoria* near Kibutz Haogen, Hasharon district, on

Fig. 3–9. 3. A young larva shown preparing its shelter on an *Alcea setosa* leaf. Santa Katarina Monastery, South Sinai, 1600 m, 22.vii.1979. **4.** *Carcharodus alceae* larval leaf pod on *Chrozophora tinctoria*. Same location and date as Fig. 1. **5.** Fully grown larva on *Chrozophora tinctoria*. Sasa, Upper Galilee, 880 m, 24.vii.2004. **6.** Winter diapausing *Carcharodus alceae* pupa. Kibutz Haogen, Hasharon district, Central Coastal Plain, Israel, 4.x.2003. **7.** Fresh *Carcharodus alceae* female from a larva which had developed on *Chrozophora tinctoria*. Sasa, Upper Galilee, 880 m, Israel, 4.viii.2004. **8.** Extrafloral nectaries of *Chrozophora tinctoria*. Attending beetles *Anthrenus* sp. (Dermestidae) and a fruit fly *Chaetorellia* sp. (Tephritidae) are possibly attracted to the nectaries. Rantis, Central Israel, ca. 200 m, 3.vii.2004. **9.** *Azanus jesous* nectaring on a flower of *Chrozophora tinctoria*. Hexagon Pool, Golan Heights, 50 m, 31.vii.2004 (Photos 8, 9: Eran Benyamini).

Fig. 10. Defoliated *Chrozophora tinctoria*. Rantis, Central Israel, ca. 200 m, 20.x.2004.
Fig. 11. 3 mm long L2 larva of *Carcharodus alceae* wandering over the stellate hairs of *Chrozophora tinctoria* leaf after being transferred from the original host-plant, *Alcea setosa*. Bet Arye, 310 m, 7.viii.2004.

the Mediterranean coastal plain in Central Israel. Both pupated on 2 October 2003. The pupae did not hatch and entered winter diapause (Fig. 6). On 29 February 2004 they were moistened with a few raindrops, but failed to hatch and later died. The precise timing of their demise is uncertain, as there were no external clues pointing to their change of condition. However, based on this very limited experience, it would appear that the late summer brood is potentially doomed; the adult's flight season is over, forcing the pupae to stay within the folded leaf. But the annual *C. tinctoria* dries up and loses all its leaves with the doomed pupae inside (Fig. 10).

This was my only experience with overwintering pupae of this species. However, in December 2004 Mr Evyatar Feingold, a young member of the Israeli Lepidopterist's Society informed me that he found a larva of *Carcharodus alceae* on *Malvella* sp. in early November 2004 in Sde-Boker, Central Negev, elev. 465 m. This larva pupated on 14 November 2004 to become the second observation of a winter-diapausing pupa. It remains to be seen if this produces a viable adult.

A t t e n d i n g   a n t s . At various locations small black ants were observed on host-plants. As the larvae were inaccessible inside their leaf pod, another reason had to be found to explain the ants' presence. (It was apparent that the ants were not attracted to the frass of the larvae). After close observation, the reason for their presence was revealed: tiny flat "buttons" on the undersides of leaves were found to be extrafloral nectaries (Fig. 8). On 31 July 2004 a large bush of *Chrozophora tinctoria* near the Hexagons Pool, on the Golan Heights, 50 m above sea level, was observed over a period of time. The flowers attracted adults of *Colotis fausta, Azanus jesous* (Fig. 9), *Tarucus balkanicus*, and one female of *Carcharodus alceae*. Numerous, small black ants were attending these special nectaries. The ants were identified by Armin Ionescu (Tel Aviv University) as *Crematogaster jehovae* Forel. It is quite reasonable to assume that their massive presence on the host-plant provided some protection to the larvae by discouraging potential parasitic wasps. However, in tropical forests where plants with extrafloral nectaries are very common (up to 53% in certain parts of Brazilian Amazon), the presence of numerous ants is a great threat to non myrmecophilous larvae

(Oliveira & Freitas, 2004). In the case of *C. alceae* larvae feeding on *C. tinctoria*, I did not find any evidence for such a threat in Israel.

Parasites and competing moths. Among ca. 20 larvae that were reared on *Chrozophora tinctoria* since 1988 none were attacked by parasites, thus demonstrating the effectiveness of their sealed leaf pod. Most of the leaf pods that were checked for *Carcharodus alceae* larvae were found to contain moth larvae. The microlepidopteran moths were identified by András Kun as Pyralidae of the family Phycitinae. The leaf pods of the moths are constructed as cylindrical webs that are not tightly sealed. In mid-June 2004 several leaf pods of *Chrozophora obliqua* were checked in Ein Gedi, Dead Sea valley (-370 m); all housed only moth larvae. One leaf pod was found to contain a white cocoon of a parasitoid wasp. *Apanteles glabratus* (Braconidae, Ichneumonidae) has been reported as parasitoid of young *C. alceae* larvae bred on *Alcea* sp. in Israel (Eisenstein 1983).

The host-plant

Chrozophora is a small genus in the large Euphorbiaceae family which contains 8100 species in 313 genera (Mabberley 2000). Twelve species are distributed from Portugal to Greece, Turkey, Cyprus, Africa and the Middle East to India and Thailand; two species grow in Southern Europe, and four in Israel: *C. tinctoria, C. obliqua* (Vahl) Ad. Juss. ex Spreng.*, C. plicata* (Vahl) Ad. Juss. ex Spreng., and *C. oblongifolia* (Del.) Ad. Juss. ex Spreng. The latter two species are rare Sudanese plants growing in the Arava Valley and Southern Negev where *Carcharodus alceae* does not fly. However, *C. obliqua* has a distribution similar to that of *C. tinctoria* and therefore may be considered another possible host-plant.

C. tinctoria is distributed along the southern coast of Europe and was reported from Portugal, Spain, the Balearic Islands, France, Corsica, Sardinia, Italy, Sicily, ex Yugoslavia, and Greece to Turkey and Crimea (USSR) (Tutin et al. 1968). It is known from North-East Africa to west and central Asia (Loutfy 2000). In 'Flora of Turkey' it is reported from the East Aegean Islands of Lesvos, Khios, Leros, Kos and Rhodos to SW & Central Asia, and to Sokotra island in South Arabia (Davis 1982). Other sources indicate its existence also in Iraq and Iran. Its reported distribution overlaps completely with that of *Carcharodus alceae* (except lower Egypt where *C. alceae* does not fly). Thus *C. alceae wissmanni* may also feed on *C. tinctoria* in Yemen.

Chrozophora tinctoria is a summer-flowering annual bush, usually up to 50 cm high, growing from March to October, from sea level to 1650 m (Turkey). It grows in deep alluvial soils, in disturbed / waste places, sandy plains (Egypt), edges of cultivated surfaces, among summer crops, or in fallow fields where it may become a weed.

The external appearance of the plant is unique; its blade ovate-rhombic leaves are greyish-to-light-green (Fig. 1). This colour is the result of numerous stellate hirsute-to-woolly leaves, with minute white hairs covering their surface.

Its scientific name means the painter's *Chrozophora* and its properties have been known for thousands of years as a source of turn-sole dye (*Bezetta rubra*, tournesol). It was also used for colouring liqueurs, wine, pastries, linen, and Dutch cheeses (Mabberley 2000).

Other butterflies feeding on Euphorbiaceae and their distribution by zoogeographical regions

Hesperiidae. Euphorbiaceae are rarely used by skippers world wide; only 9 species of the world 3660 known species are recorded by Robinson et al. (2004); one of them (*Calpodes ethlius* in the New World) is possibly an error. Four species are listed in the Afrotropical Region: *Abanitis paradisea* on *Bridelia cathartica*, *Coeliades libeon* and *Gorgyra bibulus* on *Drypetes gerrardii*, and *Parosmodes moranti* on *Bridelia* sp. Two species in the Oriental Region: *Bibasis mahintha* on *Aporusa roxburghii* and *Hasora chromus* on the widespread Castor bean (*Ricinus communis*). One species in North America (Mexico) *Arteurotia tractipennis* on *Croton niveus*, which rarely penetrates south Texas. *Calpodes ethlius*, which was reported on *Phyllanthus* sp. for the New World, is almost certainly an error (de Jong, pers. comm.). One Neotropical species: *Dyscophellus porcius* on *Croton* sp. Braby (2000) added two species in Australia: *Chaetocneme beata* on *Croton insularis* and *Chaetocneme critomedia* on *Mallotus polyadenos* and *Macaranga* sp. None was recorded until now for the whole Palaearctic Region. The new total is therefore 11 species or 0.3% of all skippers worldwide.

Papilionidae. Only four species of four genera feeding on Euphorbiaceae are known from the Neotropical and Oriental-Australian Regions. Thus, 0.7% of the world's 572 known species of Papilionidae feed on Euphorbiaceae.

Pieridae. Fifteen species of four genera are given for the Oriental, Afrotropical, and Australian Regions. Only one (*Appias drusilla*) is known from the Nearctic and none is known yet from the Neotropical and Palaearctic Regions. This is 1.23% of the world's 1222 known species of Pieridae.

Nymphalidae. Euphorbiaceae feeders are most common in this family; no fewer than 150 species in 42 genera are known nowadays. This is 2.08% of the world's known 7222 species. The family is well represented in the tropics: 52 species in 11 genera in the Afrotropical Region, 47 in 17 in the Neotropics, 33 in 12 in Central America, 23 in 14 in the Oriental Region, but only 7 in 6 in the Nearctic, 3 in 3 in Australia, and one Palaearctic (the Japanese *Athyma perius*). There are no records of Euphorbiaceae being used by nymphalids in Europe and the Middle East, though *Vanessa cardui* (recorded on *Ricinus communis* in Hong Kong) and *Danaus chrys*ippus (recorded on *Euphorbia* in West Malaysia) are candidates.

Riodinidae. Few records exist for this family (only four species are recorded by Robinson et al. 2004), but thanks to the exceptional work by DeVries (1997) on the Costa Rican butterflies, we may summarize the situation there as follows: 255 species out of the world's known 1402 Riodinids occur in Costa Rica. Of these 255, eight (3.14%) are recorded to feed on Euphorbiaceae. But since host-plants are known for only 85 species, the percentage of the Euphorbiaceae feeders may increases to 9.4% (of the known 85 species), which would be the highest in the world. The total world's known Euphorbiaceae feeders among Riodinidae are 12 species, making up 0.86%.

Lycaenidae. This extremely adaptable family stands second only to the Nymphalidae among world Euphorbiaceae feeders; 71 species in 37 genera are known Euphorbiaceae feeders, making up 1.37% of the known world's 5162 species. Most of them fly in

the Old World tropics: 30 species in 20 genera in the Oriental Region, 16 in 8 in the Australian Region, 13 in 9 for Afrotropical blues, but only 8 in 6 in the Neotropical Region, 4 in 2 for the Nearctic, and 2 in 2 for the Palaearctic Region (*Megisba malaya* in Japan and *Chilades trochylus* in south-east Europe and the Middle East.).

Tables 1 and 2 present the known number of genera and species of butterfly feeding on Euphorbiaceae together with the number of genera and species of their host-plants by world regions.

The Palaearctic Region, Europe, and the Middle East. I was the first to report usage of a member of the Euphorbiaceae family as a host-plant by a butterfly in the Middle East: *Chilades trochylus* Freyer (= *Freyeria trochylus*) (Lycaenidae) eggs and larvae were found in Israel and the Sinai Peninsula on *Andrachne telephioides* L. (Benyamini 1984, 1990 & 2002). The present article adds a second European butterfly species to the very limited list of Euphorbiaceae feeders. In the whole Palaearctic Region there are only two other known Euphorbiaceae feeders; the widespread Oriental nymphalid *Athima perius* (L.) which ranges from India to Malaysia, South China (Hong Kong), Taiwan, and Japan, and *Megisba malaya* Horsfield (Lycaenidae), another Oriental species that reaches Japan. The genus *Megisba* Moore comprises only two species; the other is the Australian *M. strongyle*, which also feeds on Euphorbiaceae.

Among world regions the use of euphorbs as butterfly larval host-plants is lowest in the Palaearctic where just four species (0.21%) out of 1896 use Euphorbiaceae.

Neotropical Region. With 71 Euphorbiaceae feeders out of 7927 species, the percentage figure of 0.89% shows this to be the second lowest region. The ratio is highest in the nymphalids, where the larvae of no fewer than 47 species (1.64%) of the known 2857 are Euphorbiaceae feeders.

Oriental Region. 64 species of 4157 represent 1.54%. Use of euphorbs is most pronounced in the Pieridae where 7 out of 307 species account for 2.28%.

Nearctic Region. Despite having only 13 feeders, these represent 1.69% of the total known 767 species. The nymphalids are again evident, with 7 (3.27%) of 214 species.

Australian Region. 26 species out of 1226 represents 2.12%, which is second only to the Afrotropical Region (2.26%). The leading family is that of the lycaenids where 16 of 407 species make up 3.93%.

Afrotropical Region. This region holds the largest concentration of Euphorbiaceae feeders with 74 species representing 2.26% of the total 3267. The use of euphorbs is most pronounced in the nymphalids where they is used by 52 (4.49%) of the known 1156 species.

Central America. Costa Rica, where euphorbs are used by 7.62% of the nymphalids and 9.4% of the riodinids (where the host-plant is known), is a "hot spot" not only for butterfly biodiversity but also for Euphorbiaceae world feeders in these two families.

Feeding on milky/ toxic host-plants

The Euphorbiaceae family has been divided recently into five subfamilies (Webster 1994a, b): the Phyllanthoideae (no milky latex), the Oldfieldioideae (no milky latex),

Tab. 1. Distribution of World butterflies that feed on Euphorbiaceae; number of species per family per zone. Sources: Benyamini (1984, 1990), Braby (2000), Canals (2003). DeVries (1987, 1997), Heppner (1991), Robinson et al. (2004), and Scott (1986). * Costa Rican numbers are also included in the Neotropical totals. ** Unknown. *** Several species of butterflies fly in more than one zone. This row presents the real numbers of known Euphorbiaceae feeders.

	Papilionidae			Pieridae			Nymphalidae			Riodinidae			Lycaenidae			Hesperiidae			Total per Region		
	Euphorbiaceae Feeders	Total Number of Species	Percentage (%)	Euphorbiaceae Feeders	Total Number of Species	Percentage (%)	Euphorbiaceae Feeders	Total Number of Species	Percentage (%)	Euphorbiaceae Feeders	Total Number of Species	Percentage (%)	Euphorbiaceae Feeders	Total Number of Species	Percentage (%)	Euphorbiaceae Feeders	Total Number of Species	Percentage (%)	Euphorbiaceae Feeders	Total Number of Species	Percentage (%)
Palaearctic	0	84	0	0	167	0	1	1083	0,09	0	16	0	2	391	0,51	1	155	0,64	4	1896	0,21
Afrotropical	0	87	0	5	174	2,87	52	1156	4,49	0	11	0	13	1402	0,93	4	437	0,91	74	3267	2,26
Oriental	2	178	1,12	7	307	2,28	23	1563	1,47	0	20	0	30	1520	1,97	2	569	0,35	64	4157	1,54
Australia	0	70	0	5	187	2,67	3	349	0,86	0	22	0	16	407	3,93	2	191	1,05	26	1226	2,12
Nearctic	0	33	0	1	64	1,56	7	214	3,27	0	25	0	4	139	2,87	1	292	0,34	13	767	1,69
Costa Rica *	0	40	0	0	70	0	33	433	7,62	8	255	3,14	1	**		1	**		43	**	
Neotropical	2	120	1,67	1	323	0,31	47	2857	1,64	12	1308	0,92	8	1303	0,61	1	2016	0,05	71	7927	0,89
Total ***	4	572	0,7	15	1222	1,23	150	7222	2,08	12	1402	0,86	71	5162	1,37	11	3660	0,3	264	19240	1,37

Tab. 2. Quantities of known Euphorbiaceae host-plants for butterfly families in the world's major zoogeographical zones (Gen.=Genera ; Sp.=Species). Sources: Benyamini (1984, 1990), Braby (2000), Canals (2003), DeVries (1987, 1997), Robinson et al. (2004) & Scott (1986). * Several species of butterflies fly in more than one zone. This row presents real numbers.

	Papilionidae				Pieridae				Nymphalidae				Riodinidae				Lycaenidae				Hesperiidae			
	Butterflies		Hosts		Butterflies		Hosts		Butterflies		Hosts		Butterflies		Hosts		Butterflies		Hosts		Butterflies		Hosts	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
Palaearctic	0	0	0	0	0	0	0	0	1	1	2	4	0	0	0	0	2	2	3	4	1	1	1	1
Afrotropical	0	0	0	0	3	5	4	5	11	52	18	37	0	0	0	0	9	13	8	8	4	4	2	2
Oriental	2	2	2	2	3	7	5	10	14	23	20	35	0	0	0	0	20	30	11	20	2	2	2	2
Australia	0	0	0	0	2	5	3	7	3	3	3	3	0	0	0	0	8	16	7	14	1	2	2	2
Nearctic	0	0	0	0	1	1	1	1	6	7	6	10	0	0	0	0	2	4	1	2	1	1	1	1
C-America	0	0	0	0	0	0	0	0	12	33	7	20	6	8		5	1	1	1	1	1	1	1	1
Neotropical	2	2	2	2	1	1	1	1	17	47	14	38	4	5			6	8	1	2	1	1	1	2
Total *	4	4	4	4	4	15	7	22	42	150	36	118	7	12			37	71	24	46	11	12	9	11

the Acalyphoideae (latex absent), the Crotonoideae (latex reddish or yellowish-to-milky), and the Euphorbioideae (latex whitish, often caustic or poisonous).

Table 3 presents the number of butterfly species/feeders and their Euphorbiaceae host genera. The leading subfamily is the Acalyphoideae where 22 genera are used as host-plants by 141 species of butterfly. Phyllanthoideae are second with 13 genera and 81 butterflies, followed by Crotonoideae 6/ 52, Euphorbioideae 7/ 25 and Oldfieldioideae 1/ 2.

We calculated the number of genera used and their percentage in each subfamily. The results are presented in Tab. 4 with the total number of Euphorbiaceae feeders per subfamily.

Though toxicity of each plant genus within the subfamilies is not considered, the accumulated results of Tab. 4 suggest that butterfly preference among the Euphorbiaceae subfamilies declines as plants become more toxic. It also means that butterfly adaptation to toxic hosts, which may provide chemical defence, is slow, limited, and possibly problematic.

Rizk's (1987) phytochemical analysis of the Euphorbiaceae specifies the toxic compounds in this family; many of these host-plant genera appear in Tab. 3. It is important to note that Rizk's work presents chemicals that were found in specific plants; it does not mean that other plants including host-plants of the same genera have the same compounds. However, for the preliminary analysis in Tab. 5 I assume that each genus is homogeneous regarding chemical ingredients of its species.

Let us examine briefly the more common toxic compounds that were found in the Euphorbiaceae (Tab. 5):

Over 55 Terpenoids (tetra- and pentacyclic) have been identified; mostly in the latex of *Euphorbia* spp., but also in other parts (bark, leaves, flowers, stems, and roots). Such compounds were found also in the plant genera *Macaranga*, *Croton*, *Phyllanthus*, *Antidesma*, *Glochidion*, *Bridelia*, and *Sapium*.

Fatty acids have been reported from relatively few species. These include *Euphorbia* sp., *Trewia* sp. and *Hevea* sp.

Phenolic substances of the following types were identified: Flavonoids in several *Euphorbia* spp., Coumarins in *Mallotus* spp. and *Euphorbia* sp., Lignans in *Phyllanthus* sp., Tannins in *Mallotus* sp., *Euphorbia* sp., *Phyllanthus* sp., *Sapium* sp. and *Acalypha* sp., Quinones in *Acalypha* sp., *Euphorbia* sp., and *Hevea* sp., Phenolic acids in *Euphorbia* sp. and *Ricinus communis*.

Several types of Alkaloids exist especially in *Croton*, *Phyllanthus*, and *Securinega* species. Imidazole alkaloid was found only in *Glochidion* sp. Pyrimidine and Guanidine alkaloids were isolated only from *Alchornea* sp. Several Quinolizidine alkaloids were found in *Phyllanthus* and *Securinega* sp. Glycoalkaloids were found in *Euphorbia* sp.

Cyanogenic glucosides have been identified in Phyllanthoideae and Euphorbioideae. The taxa of these tribes can produce hydrocyanic acid. Several species of the following genera were found to be cyanogenic: *Andrachne*, *Bridelia*, *Euphorbia*, *Gymnanthes*, *Hevea*, *Manihot*, *Phyllanthus*, and *Securinega*.

Several *Euphorbia*, *Antidesma*, and *Croton* species are used as fish and arrow poisons. Extensive medicinal use of Euphorbiaceae plants has been known since antiquity. While many of these plants are extremely toxic, details of their use are beyond the scope of

this article. However, the last column in Tab. 5 indicates which host-plant genus has medicinal importance.

Calculating the percentage of known toxic species in certain genera, and thus assuming which genus is toxic, yields interesting preliminary results for the use of toxic Euphorbiaceae genera as host-plants (Tab. 5). While 42.55% of the Acalyphoideae known host-plants are toxic (56.79% is given for the Phyllanthoideae), the figures for the subfamilies with toxic latex are much higher: 60% for Euphorbioideae and 92.31% for Crotonoideae. Further detailed research is needed to analyze these interesting results.

Lack of warning coloration

A straightforward comparison with other feeders of toxic plants, e.g. Papilionidae larvae on Aristolochiaceae and Danainae larvae on Asclepiadaceae, highlights other interesting differences: *Carcharodus alceae* and its larvae do not have warning coloration while it is highly pronounced in Papilionidae and Danainae.

Tab. 3. Usage of Euphorbiaceae subfamilies and genera by Rhopalocera. Sources: Tabs. 1–2, Mabberley (2000), Robinson (2004 and pers. comm.), DeVries (1997), G. L. Webster (1994a, 1994b, pers. comm.). * These figures include butterflies that feed on more than one Euphorbiaceae genus or tribe.

Euphorbiaceae subfamily	Genus	Papilionidae	Pieridae	Nymphalidae	Riodinidae	Lycaenidae	Hesperiidae	Total	percent of world Euphorbiaceae feeders*
I. Phyllanthoideae	*Antidesma*			3		1		4	**26,91%**
No milky latex	*Drypetes*		12	3		3	2	20	
	Phyllanthus		5	3		1		9	
	Securinega			3				3	
	Hyeronima			1	1			2	
	Bridelia		1	5		4	2	12	
	Aporusa						1	1	
	Uapaca			2		1		3	
	Baccaurea					3		3	
	Glochidion			6		9		15	
	Breynia		3	2		1		6	
	Andrachne					1		1	
	Flueggea			2				2	
Subtotal		0	21	30	1	24	5	**81**	
II. Oldfieldioideae	*Petalostigma*			1		1		2	**0,66%**
No milky latex									
Subtotal		0	0	1	0	1	0	**2**	

Tab. 3. Continued.

III. Acalyphoideae	*Clutia*					1		**1**	**46,84%**
Latex absent, leaves often petiolar	*Chrozophora*						1	**1**	
or laminar glands	*Alchornea*			7		2		**9**	
	Acalypha			8	1			**9**	
	Macaranga	1		8		7	1	**17**	
	Mallotus			4		5	1	**10**	
	Ricinus		2	8	3		1	**14**	
	Trewia					1		**1**	
	Dalechampia			38				**38**	
	Conceveiba			1	1			**2**	
	Erythrococca					1		**1**	
	Micrococca					1		**1**	
	Bernardia					1		**1**	
	Aparisthmium			2				**2**	
	Claoxylon			1				**1**	
	Cnesmone			1				**1**	
	Platygyna			1				**1**	
	Pterococcus			1				**1**	
	Tetracarpidium			2				**2**	
	Tragia			25				**25**	
	Adelia			1				**1**	
	Adriana					2		**2**	
Subtotal		1	2	108	5	21	4	**141**	
IV. Crotonoideae	*Hevea*		1	1		2		**4**	**17,28%**
Latex reddish or yellow to milky	*Manihot*			2				**2**	
	Codiaeum			1				**1**	
	Croton	1		30	4	4	3	**42**	
	Omphalea				2			**2**	
	Trigonostemon					1		**1**	
Subtotal		1	1	34	6	7	3	**52**	
V. Euphorbioideae	*Excoecaria*			3				**3**	**8,31%**
Latex whitish, often caustic or	*Sapium*			10				**10**	
poisonous	*Euphorbia*	1		2		1		**4**	
	Actinostemon	1						**1**	
	Gymnanthes			1				**1**	
	Maprounea			2				**2**	
	Sebastiana			4				**4**	
Subtotal		2	0	22	0	1	0	**25**	

Tab. 4. Euphorbiaceae subfamily preference by feeding butterfly species. [1] including butterflies that feed on more than one genus or subfamily.

Euphorbiaceae	No. of genera used as host-plants and their percentage within each subfamily	No. of species of feeding butterfly larvae [1]	Preference %
Phyllanthoideae	13 (22.4%)	81	26.91
Oldfieldioideae	1 (3.6%)	2	0.66
Acalyphoideae	22 (18.6%)	141	46.84
Crotonoideae	6 (9.8%)	52	17.28
Euphorbioideae	7 (16.6%)	25	8.31
Total	49 (15.9%)	301	100.00

The lack of warning coloration in *C. alceae* suggests that its acceptance of Euphorbiaceae is a very recent one. Most Rhopalocera larvae of Euphorbiaceae feeders appear to be cryptic, yet the recognized association of warning colours and toxicity in other species indicates that the Euphorbiaceae feeders will possibly develop warning coloration in the future. It has already happened in the conspicuous and possibly toxic larva of the hawkmoth *Hyles euphorbiae* (Sphingidae). It is our lucky privilege being able to follow this change in real time and to measure how many years it will take for these warning colours to develop. I expect it to be much shorter than we can guess or estimate nowadays. More than that, the change will possibly be pronounced only in the *Chrozophora* feeders while other *C. alceae* will not change. Does this also foretell a future speciation event in *C. alceae*?

Switching from Malvaceae to Euphorbiaceae - Summary

On 4 August 2004 in Bet Arye, Central Israel, elevation 310 m, foodplants were in short supply. Five first and second instar larvae and one un-hatched egg were found on a tiny *Alcea setosa* plant having only three leaves, each of 5 cm diameter. It is obvious that in such circumstances, with no other foodplant available, larvae will starve to death. This seasonally repeated shortage of host-plants in the dry Mediterranean summer, is the key driver for searching and switching to alternative plants. The five young larvae with their tiny leaves were transferred into separate breeding vials where fresh *Chrozophora tinctoria* plants were added. Three larvae accepted it quite willingly and were observed feeding on young leaves on 7 August. The other two wandered restlessly (Fig. 11), and eventually were seen accepting the *Chrozophora* reluctantly, and tentatively, on 11 August. Closer observation suggested that the hairs on the plant acted as mild discouragement to feeding. Finally, three adults hatched between 26 August and 2 September 2004. This experiment demonstrated that all the larvae switched from *Alcea* to *Chrozophora* but the final rate of success was three out of five, measured in terms of transition from larva to adult, which is 60%. The limited observation, if repeated

under natural conditions, suggests that acceptance of this host- plant developed over the last sixteen years from 0% in 1988 to 60% in 2004. Field observations indicate that eggs which were laid directly on the *Chrozophora* developed normally, though some adults failed to emerge successfully. Switching to this summer host-plant appears to have the dubious benefit of extending the breeding season to the autumn, so that larvae feeding in late-season produce pupae which then find themselves in the cold, unfavourable climate of early winter and are forced to overwinter. We still do not know if they can survive the winter in this stage of their life cycle.

Are we witnessing a switching process (or an acceptance of an alternative host-plant) that has started in the recent past, and is still evolving? Lack of warning coloration in both larvae and adults support this hypothesis. Is it linked to the desiccation of our biotopes due to the greenhouse effect? We postulate that both processes are happening within the same timetable.

Tab. 5. Toxic chemicals of the Euphorbiaceae host-plants of butterflies.

Euphorbiaceae		Terpenoids	Fatty acids	Phenolic substances	Alkaloids	Cyanogenic Glucosides	Medicinal plants	Total species feeders	% of toxic genera *	% of plant species which are toxic and used as host-plants**
I. Phyllanthoideae	*Antidesma*	v					v	4	53,80	56,79
No milky latex	*Drypetes*							20		
	Phyllanthus	v		v	v	v	v	9		
	Securinega				v	v		3		
	Hyeronima							2		
	Bridelia	v				v	v	12		
	Aporusa						v	1		
	Uapaca							3		
	Baccaurea							3		
	Glochidion	v			v		v	15		
	Breynia						v	6		
	Andrachne					v	v	1		
	Flueggea			v	v		v	2		
Subtotal								81		
II. Oldfieldioideae	*Petalostigma*							2	0,00	0,00
No milky latex										
Subtotal								2		

Tab. 5. Continued.

III. Acalyphoideae	*Clutia*							v	1	27,27	42,55
Latex absent, leaves often	*Chrozophora*								v	1		
petiolar or laminar glands	*Alchornea*					v			v	9		
	Acalypha				v		v		v	9		
	Macaranga	v							v	17		
	Mallotus				v				v	10		
	Ricinus				v	v			v	14		
	Trewia		v			v			v	1		
	Dalechampia									38		
	Conceveiba									2		
	Erythrococca								v	1		
	Micrococca									1		
	Bernardia									1		
	Aparisthmium									2		
	Claoxylon									1		
	Cnesmone									1		
	Platygyna									1		
	Pterococcus									1		
	Tetracarpidium									2		
	Tragia								v	25		
	Adelia									1		
	Adriana									2		
Subtotal										141		
IV. Crotonoideae	*Hevea*			v	v			v		4	50,00	92,31
Latex reddish or yellow to milky	*Manihot*				v			v	v	2		
	Codiaeum									1		
	Croton	v			v	v			v	42		
	Omphalea									2		
	Trigonostemon									1		
Subtotal										52		
V. Euphorbioideae	*Excoecaria*								v	3	42,85	60,00
Latex whitish, often caustic or poisonous	*Sapium*	v			v				v	10		
	Euphorbia	v	v		v	v	v		v	4		
	Actinostemon									1		
	Gymnanthes						v			1		
	Maprounea									2		
	Sebastiana								v	4		
Subtotal										25		

Finally, Mabberley (1997) in his discussion on similarities of the five Euphorbiaceae subfamilies noted: "The seed structure....of the others [incl. *Chrozophora*] show more affinity with.....Malvaceae...". Does it mean that this switching was inevitable?

Acknowledgements

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